

February 5, 1907.

His Grace THE DUKE OF BEDFORD, K.G., President,
in the Chair.

Mr. F. Martin Duncan, by permission of the Charles Urban Trading Co., Ltd., gave a cinematograph exhibition of animals in the Society's Gardens and other zoological subjects, chiefly the life-history of Insects.

Mr. Oldfield Thomas, F.R.S., F.Z.S., exhibited a collection of Mammals and Birds from the Islands of Saghalien and Hokkaido, N. Japan, made by Mr. Malcolm P. Anderson in carrying out the Duke of Bedford's Exploration of Eastern Asia. Mr. Thomas proposed to give a full account of the Mammals on a later occasion.

Dr. W. T. Calman, F.Z.S., read a paper entitled "On new or Rare Crustacea of the Order Cumacea from the Collection of the Copenhagen Museum. Part I. The families *Bodotriidae*, *Vann-tompsoniidae*, and *Leuconidae*."

This paper will be published entire in the 'Transactions.'

The following papers were read:—

1. The Origin of the Lateral Horns of the Giraffe in Foetal Life on the Area of the Parietal Bones. By E. RAY LANKESTER, M.A., D.Sc., LL.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum.

[Received February 5, 1907.]

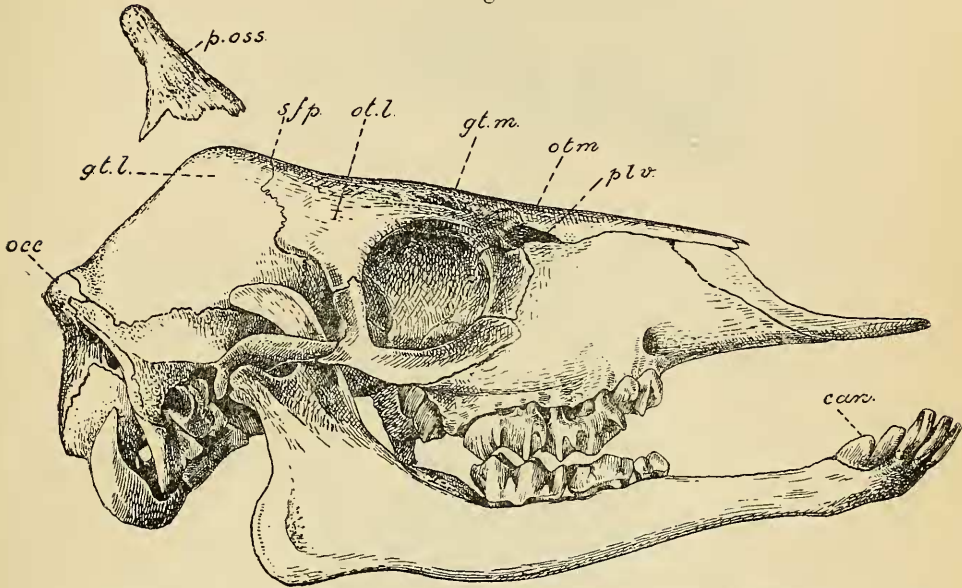
(Text-figures 24-36.)

A remarkable and wide difference between the Giraffe and the Okapi is constituted by the position and relation of the lateral horns in these two animals in regard to the bones of the skull. As I pointed out in my memoir on the Okapi read in 1901 (Trans. Zool. Soc. vol. xvi. p. 279), the bony horn-cone of that animal is attached to the frontal bone, and it is the frontal bone which is raised into a boss for its support, whilst even in the hornless skulls supposed to be those of the female these frontal bosses are present. On the other hand, in the young Giraffe the main axis of the lateral "ossicone"* falls within the area of the parietal bone

* I use the term "ossicone" in the present paper for the independently ossifying bony cones which are found in Okapi and Giraffe on the frontal and parietal areas and in the Giraffe also in a median position. In my memoir of 1901 I spoke of such structures as "ossicusp," a term which I now wish to apply more generally, reserving the term "ossicone" for the peculiar separately ossifying cones of the Giraffidae.

(text-fig. 24). The wide-spreading base of the cone-like ossicone subsequently encroaches, it is true, over a large portion of the frontal bone. In the adult both the parietal and the frontal are

Text-fig. 24.



Lateral view of the skull and lower jaw of a very young Giraffe, measuring 30·8 centimetres from the occiput to the anterior border of the premaxilla: preserved in the British Museum. The drawing is five-twelfths of the natural size.

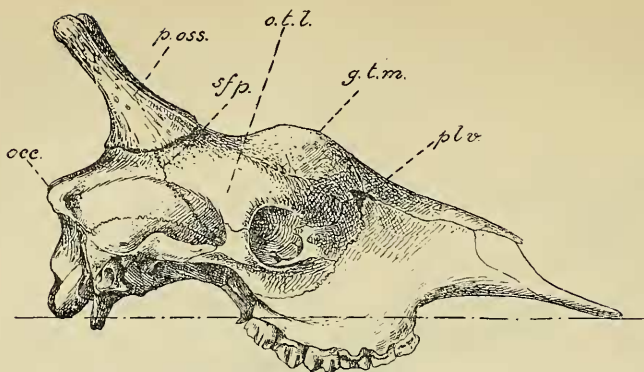
occ., occipital crest; *gt.l.*, Giraffine conical tumescence of the parietal bone, above which is developed the lateral ossicone (*p.oss.*); *sfp.*, the fronto-parietal suture; *ot.l.*, position of the lateral tumescence of the Okapi, absent here; *gt.m.*, position of the median frontal tumescence of the Giraffe, which in this young specimen is still entirely undeveloped; *ot.m.*, position of the median tumescence of the Okapi's skull (basinasal); *pl.v.*, prelacrymal vacuity; *can.*, bifoliate canine (deciduous dentition).

(From Trans. Zool. Soc. vol. xvi. p. 293.)

enlarged and tumescent, and both enter largely into the composition of the lateral horn of the adult Giraffe (text-figs. 25 & 33). The whole form of the skull is rendered different in the two genera by this relationship of the ossicone to the frontal exclusively in the one, to the parietal primarily but not exclusively in the other (see text-figs. 26 & 27).

In a skull of a very young Giraffe (text-fig. 24), probably about a year old, preserved in the British Museum, the lateral ossicone is seen to rest almost entirely on the parietal. A transverse section (text-fig. 28, p. 104) shows that the anterior margin of the enlarging base of the bone constituting the ossicone has spread—

Text-fig. 25.

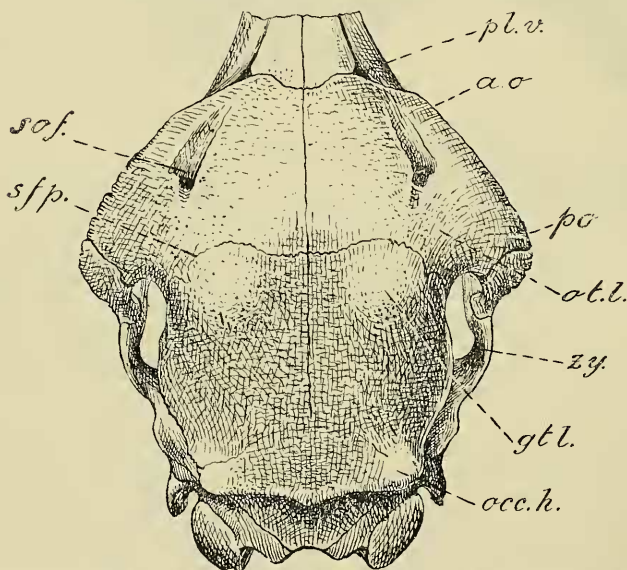


Lateral view of the skull of a Giraffe, about two-thirds grown.

occ., occipital crest; *p.oss.*, parietal ossicone (epiphysis) overlying the parietal conical upgrowth and spreading on to the frontal bone; *sfp.*, fronto-parietal suture; *o.t.l.*, position of the lateral frontal tumescence in the Okapi, absent here; *g.t.m.*, the characteristic median tumescence of the Giraffe's frontal, devoid in this specimen of any secondary cap or epiphysis, absent in the Okapi; *pl.v.*, the prelacrymal vacuity.

(From Trans. Zool. Soc. vol. xvi. p. 284.)

Text-fig. 26.



View from above of the fronto-parietal region of the skull of a very young Giraffe. The parietal epiphyses were already ossified, but separable, and are here removed.

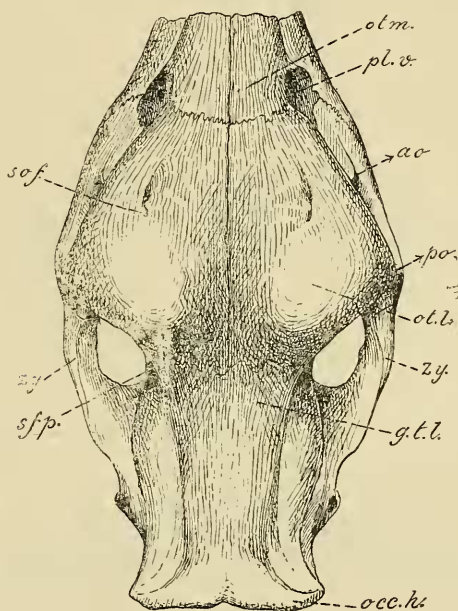
occ.h., exostosis of the occipital crest, which in some adult Giraffes forms a second pair of "horns" (five-horned Giraffe); *gtl.*, the Giraffine lateral tumescence, seen here to originate in the parietal bone, which carries the conical ossicone and forms the Giraffe's paired "horns"; *ot.l.*, the position of the Okapi's lateral tumescence of the frontal bone, absent in Giraffe; *zy.*, zygomatic arch; *po.*, posterior angle of the orbit; *ao.*, anterior angle of the orbit; *pl.v.*, prelacrymal vacuity; *sof.*, supraorbital fossa; *sfp.*, fronto-parietal suture.

(From Trans. Zool. Soc. vol. xvi. p. 291.)

invaded as it were—the area of the frontal bone to a very slight extent.

It seemed hardly possible to doubt that the ossicone of the Giraffe takes its origin within the area of the parietal bone, but that conclusion was forbidden by the explicit statement of the late Sir Richard Owen who, in a paper published sixty-seven years ago (1840) in the 'Transactions' of the Zoological Society, described a newly-born Giraffe which had died in the Gardens of the Zoological Society. Owen there states that he found the lateral horns of this Giraffe to be definitely attached to the *frontal* bone, and to that

Text-fig. 27.



View from above of the fronto-parietal region of the skull of an immature Okapi.

occ.h., angle of the occipital crest; *g.t.l.*, position of the lateral tumescence of the parietal which supports the paired ossicones of the Giraffe, absent here; *o.t.l.*, the Okapian tumescence of the frontal which supports the paired ossicones of the Okapi; *zj.*, the zygomatic arch; *po.*, posterior angle of the orbit; *ao.*, anterior angle of the orbit; *pl.v.*, prelacrymal vacuity; *otm.*, the slight median tumescence of the base of the nasals of the Okapi; *sof.*, supraorbital fossa; *sfp.*, the fronto-parietal suture.

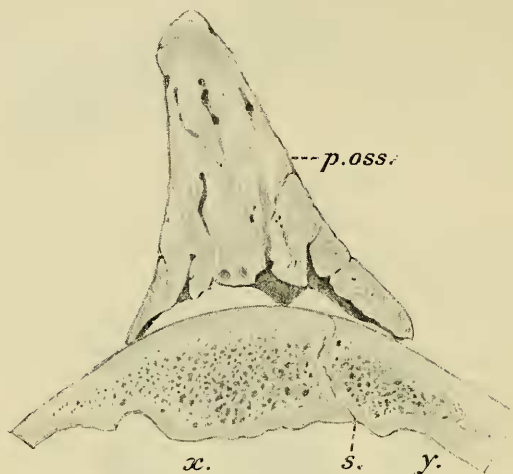
For comparison with text-figure 26.

(From Trans. Zool. Soc. vol. xvi. p. 290.)

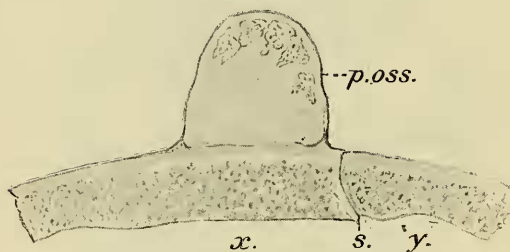
bone exclusively. He gives the drawing, which is copied in text-fig. 29, p. 104. He draws attention to the suture (*s*) separating the two bones seen in section, and he states that *x* is the frontal bone and *y* the parietal. He arrives at the conclusion that whilst the lateral horns of the Giraffe are seen thus to originate as do the horns of all other Pecora, in connection with the frontal bone,

yet that in the Giraffe the growing horn must spread from its original position, and in fact take up a new position on the parietal, with which he recognises that it is largely in contact in adult life.

Text-fig. 28.



Text-fig. 29.



Text-fig. 28.—Sagittal section through the bony tissue of the ossicone and the roof of the skull of a very young Giraffe (same specimen as that drawn in text-fig. 24). Drawn of the natural size.

p.oss., the ossicone; *s.*, the parieto-frontal suture; *x.*, the parietal bone; *y.*, the frontal bone.

Text-fig. 29.—Copy of the drawing (natural size) of a sagittal section through the ossicone and the roof of the skull of a newly-born Giraffe, published by the late Sir Richard Owen in the *Trans. Zool. Soc.* 1840.

p.oss., the ossicone; *s.*, the parieto-frontal suture; *x.*, stated to be a "frontal" by Owen but actually parietal; *y.*, stated to be "parietal" by Owen but now shown to be frontal.

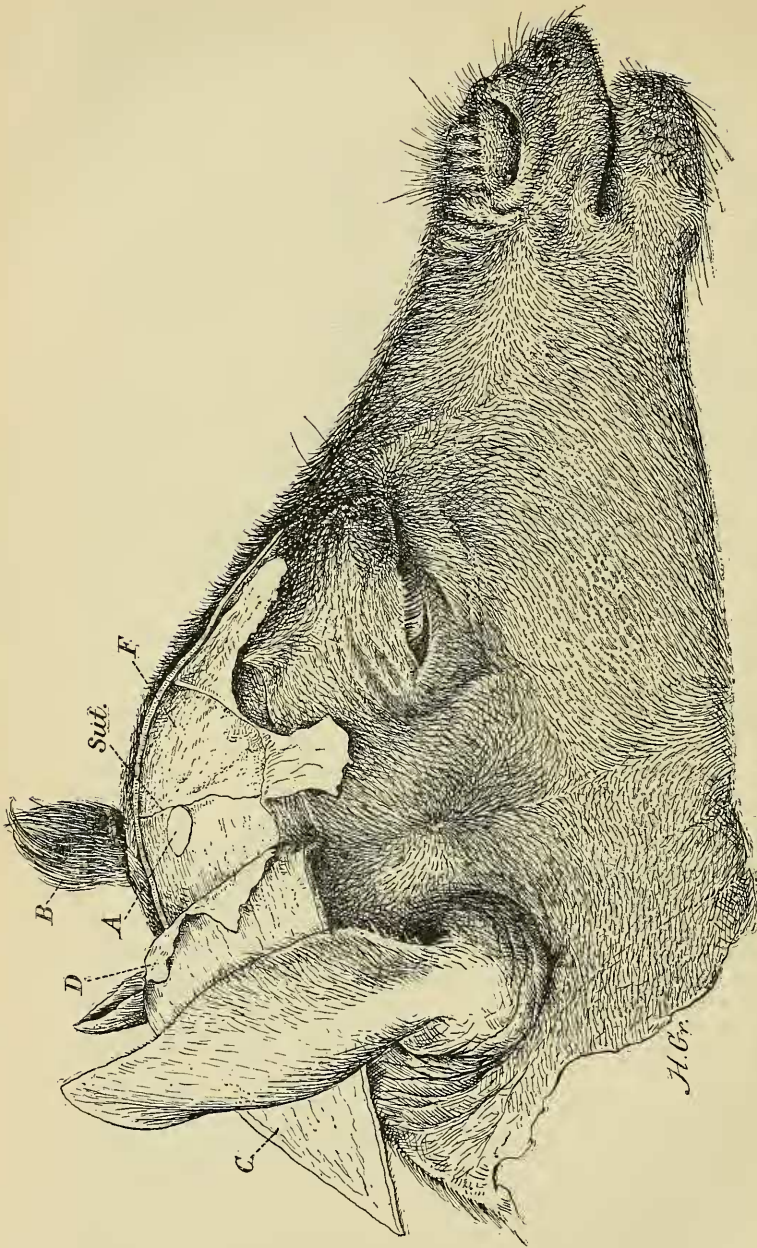
I felt considerable doubts as to the correctness of this observation, and obtained through the kindness of Prof. Stewart some

five years ago the actual skull of the newly-born Giraffe examined by Owen, and still preserved at the Royal College of Surgeons. The whole of the frontal and parietal regions had been cut away from the skull and the pieces could not be found. There was no evidence to be obtained from the specimen as to what really was the nature of the bone *x* (in text-fig. 29) and the bone *y*. I formed the hypothesis that Owen had had the horn-bearing region cut out and a section made by an assistant. The section is that which he figured and is here copied. But the piece having been detached from the rest of the skull, Owen seems to have mistaken right for left and back for front, so that in reality the bone marked *x* is the parietal and the bone marked *y* is the frontal; and the young horn or ossicone is resting on the parietal as it does in the later stages of growth, and not on the frontal as supposed by Owen.

I could not test the truth of this hypothesis without examining myself a newly-born Giraffe or a well-advanced foetus, and accordingly I have made efforts to obtain such a specimen by application to the officials of the late African Department of the Foreign Office and to those of the Colonial Office, as well as to naturalists and sportsmen. No newly-born or foetal Giraffe came to hand, nor could I hear of one as being preserved in any Museum in Europe. Accordingly I was very grateful when last summer our Secretary was able to place at my disposal the foetal Giraffe which was removed from its mother after her death in the Gardens in April 1906. This foetal Giraffe was figured and described in a general way by Mr. Beddard (Proc. Zool. Soc. 1906, p. 626), but the examination of the skull was kindly left to me. The dead mother of this foetus was a South-African (Transvaal) Giraffe (*G. camelopardalis wardi*) and the father a Kordofan specimen (*G. camelopardalis antiquorum*). Mr. Beddard has given the dimensions of the foetus, and has estimated that it had probably completed two-thirds of its foetal life. He has pointed out and figured the large size of the incipient lateral horns, and their free extremities tufted with long hair, and has noted that their substance is of a gristle-like consistency.

Soon after I received the specimen, the integument (C) was reflected from the right side of the fronto-parietal region of the head, under my supervision, by my assistant Dr. Ridewood; and by subsequent reflection of part of the periosteum the view obtained which is given in text-figure 30. The integument of the right side of the head (C) was thrown back, and the periosteum of the parietal bone was reflected (D) excepting that part lying beneath and forming the base of the right lateral horn. This was pinned down and cut away from the rest of the periosteum, leaving it as an oval area A, marking exactly the position of the ossicone (fibrous and soft) on the parietal bone. In the drawing the suture separating the frontal from the parietal bone is seen (*sul.*), and it is demonstrated that the base of the young lateral horn or ossicone is wholly within the area of the parietal bone, to the periosteum of which it is loosely attached by connective tissue.

Text-fig. 30.



Drawing of the right side of the head of the fetal Giraffe described in the text, of three-fifths the natural size. The integument carrying the right "horn" has been reflected (C) and all of the subjacent periosteal membrane D, except an oval patch A corresponding exactly to the base of the right horn which is itself out of sight on the other side of the reflected flap of integument. F is the frontal bone; *Sut.* is the fronto-parietal suture; the naked bony surface upon which the oval patch of periosteum A is lying is the parietal bone; B is the hairy horn-rudiment of the left side.

The substance of the young ossicone was free from osseous deposit but of a tough consistence. Microscopic sections showed it to consist of a fibro-trabecular tissue with abundant interspersed cellular elements.

The dissection as here presented definitely establishes the fact that the site of origin of the lateral horns or ossicones of the Giraffe is entirely within the area of the parietal bone. The supposition that Sir Richard Owen had by inadvertence reversed the cut-out portion of the fronto-parietal area of his newly-born Giraffe, and had thus identified parietal as frontal and frontal as parietal, is confirmed. The importance of the distinction between the genus *Giraffa* and the genus *Okapia*, arising from the parietal position of the lateral ossicones in the former and their frontal position in the latter, is thus placed on a firm basis, since it is shown that at a stage of growth even earlier than that of birth the "forecast" or rudiment of the Giraffe's lateral bony cone (ossicone) is placed and attached absolutely and solely within the area of the parietal bone.

Text-fig. 31.



The left "horn" of the foetal Giraffe, drawn of the natural size.

- A. Seen from behind (postero-external face).
 B. Seen from in front (antero-internal face).

The form of the soft unossified forecasts of the lateral ossicones in this foetal Giraffe is worthy of further notice. As shown in Plate V. accompanying a later paper in this volume, and in the text-figure here given (fig. 31), the upgrowth is of considerable size, is compressed so as to give a narrow oblong area in transverse section, and is set on the head so that the elongated basal area has an oblique position, with its long diameter directed backwards and inwards towards the median line. The surface of the ossicone-forecast is covered with hair, which is very coarse and long at the free upstanding margin, as shown in text-fig. 31.

The text-figure 32 also shows that three of the dark hair-bands are disposed around the base of the young ossicone. The great

Text-fig. 32.

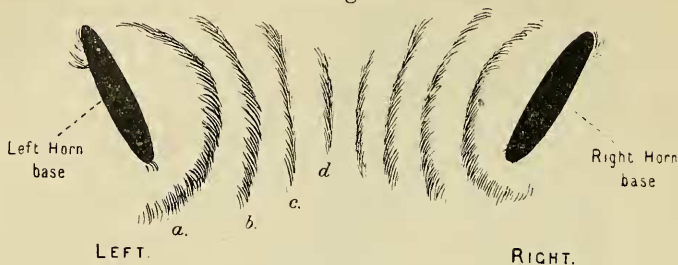


Diagram to show the flattened plate-like form and the orientation of the horns of the fetal Giraffe.

a, b, c, d. The four left-side inter-cornual colour-bands of the pelage.

lateral compression or flattening of the young structure is remarkable as compared with the fuller circular contour of a transverse section after ossification has advanced.

Possible Relations of the Giraffid Ossicones to the bony Horn-cores of Bovidae and the Antlers of Cervidae.

In my memoir describing Sir Harry Johnston's specimens of Okapi, I ventured on some speculations as to the relationships of the bony growths called horns and antlers in the Pecora. These speculations were vitiated by the uncertainty of existing knowledge as to the actual embryological origin of the structures compared. They assumed the origin of the horn-cores of Bovidae as separate rudiments which become united to the osteogenetic tissue of the frontal bone at an early period of development.

Although convincing histological accounts of their development are not yet in existence, it seems to result from the observations of Dürst that the horn-cores of Bovidae are not of independent origin, but are actual outgrowths of the osteogenetic tissue of the frontal bone. The same origin appears to hold for the horn-style or column which supports the antler of the Cervidae.

It is unfortunately the fact that our knowledge of the early embryological history of the "ossicones" of the Giraffe and Okapi is still more defective. All we know is (1) that in Owen's newly-born Giraffe the rudimentary unossified ossicone was separated (as shown in text-fig. 29) by the dense periosteal membrane from the subjacent parietal bone; (2) that in the fetal specimen of two-thirds time here described the soft forecast of the ossicone was equally cut off from the subjacent parietal bone by dense

periosteum; and (3) that in a much younger dried skull there is no indication on the cranial wall of any "outgrowth."

We shall not be in a position to speak definitely until other foetal Giraffes of younger stages have been examined by proper histological methods; but it seems legitimate to consider the lateral ossicones of the Giraffe, and therefore of the Okapi, as originating in a fibrous osteogenetic mass which gives rise to a protrusion of the integument and originates in the connective tissue of the integument rather than in the osteogenetic tissue of the cranial roof, from which it is separated by a dense membranous periosteum.

The lateral ossicones of the Giraffe appear to have the same nature and mode of origin as has the centrally-placed ossicone of the same animal. This median ossicone is variable in size, and does not appear until many years after birth when growth is nearly complete. The histological processes by which the median ossicone is formed have never yet been studied, but it is practically certain that it forms not as an outgrowth of the bone of the cranial roof, but as a "dermal" or tegumentary growth external to and independent of the cranial bone.

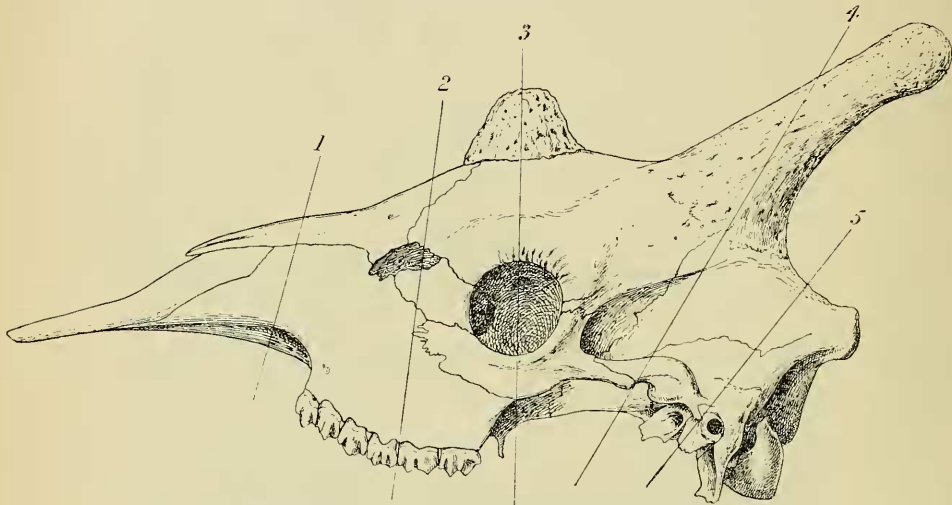
The same process which leads in the Giraffe to the formation of a median ossicone, in some cases becomes specially active and leads to the formation of additional "supernumerary" sub-tegumental ossifications. Thus two such of smaller size than the normal median ossicone are seen in the median line in a skull of Giraffe in the British Museum, in which bony deposits on the margin of the orbit are also seen. The skull of Okapi brought by Capt. Boyd Alexander from the Welle River shows such an exceptional sub-tegumental bony deposit on the margin of each orbit; and it is to be noticed that both in Giraffes and Okapis in old individuals the base of each ossicone spreads very widely as a thin encrusting layer, so as to involve much of the frontal in specimens of Giraffe and a large surface of the parietal in the case of Okapi.

These superficial ossicones and their outspreading marginal growths of the Giraffidæ cannot be accurately marked off in later life, although they can be separated in earlier life, from the highly important upgrowths or "tumescences" (as I previously called them) of the cranial bones over which they lie. The completed lateral horn of the Giraffe consists very largely of a conical upgrowth of the parietal bone, and also of the frontal bone—occupied by an air-sinus—developed between the tabulæ of the bone. The basal region of the upgrowth involves the frontal bone more largely than the parietal. The originally independent ossicone contributes but a small amount to the whole bulk of the structure. It forms merely the terminal knob, and is fitted over the tumescence like a superficial investment which dwindles in thickness as it descends the cone until it becomes a mere film.

The position of the lateral and median ossicones in an adult

(though not senile) Giraffe, and the relation of the sinus of the parietal and frontal to the lateral horn, is shown in the figures (text-figs. 33 & 34) which were prepared from photographs of sections of a skull made under my direction. It will be observed that it is not possible in such sections to distinguish the line of ankylosis of the separate bones; we can only guess somewhat vaguely as to what belongs to each of the three elements fused together, viz., ossicone, parietal, and frontal.

Text-fig. 33.



Skull of Giraffe, left side; key-figure, a little larger than one-sixth (linear) of the natural size, showing the directions in which the skull was cut.

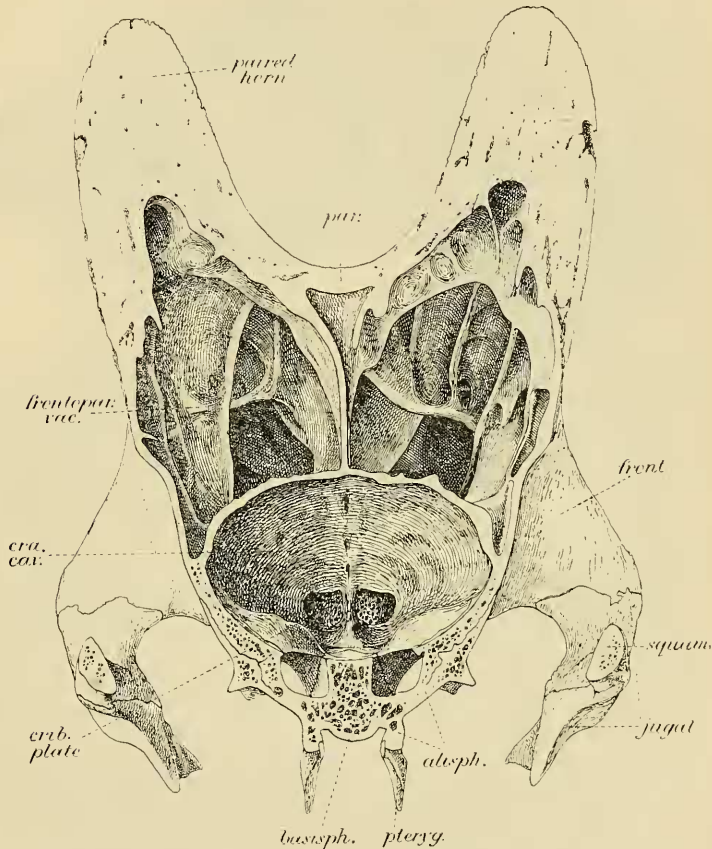
(From the Proc. Zool. Soc. London, 1904, vol. i. p. 151.)

Thus we see that the "ossicone" of the adult Giraffe is essentially but a cap of bony substance fitting over the great upgrowth or conical tumescence of the cranial wall—at the first most marked in the parietal area,—and that it makes its first appearance as a solid growth of fibrous tissue resting on the flat cranial roof. The same conclusion may legitimately be drawn from what we can see of the early and later conditions of the ossicone in Okapi*.

* The tumescence of the frontal bone of each side in Okapi, which ankyloses with the ossicone overlying it, is of considerable volume, like those to which the parietal gives rise in the Giraffe. I shall have an opportunity of describing this structure more fully hereafter. At the present moment I desire to draw attention to a curious fact with regard to the rudiment of a median horn in Okapi. The base of the nasal bone gives rise to a small but well-marked median tumescence in the Okapi. I described this in Sir Harry Johnston's specimen (Trans. Zool. Soc. vol. xvi.). In horn-bearing skulls of Okapi this is more pronounced than in the hornless specimens; it

Since it is clear then that the Giraffe's horns comprise two bony factors, the question arises which of the two corresponds with the horn-core of Bovidae, or whether either or neither had such a correspondence.

Text-fig. 34.

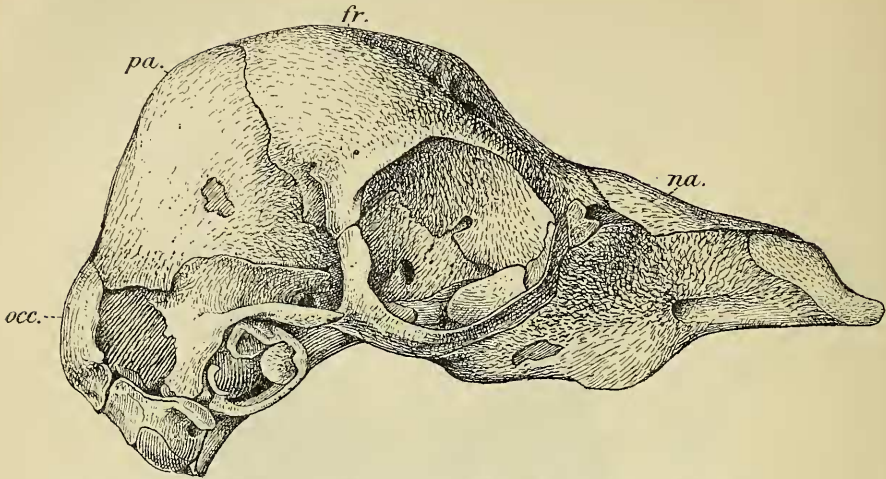


View, looking forwards, of the skull cut in the direction of the line 4 in text-fig. 33.
One-third (linear) of the natural size.

(From the Proc. Zool. Soc. London, 1904, vol. i. p. 154.)

is more strongly marked in the horn-bearing skull of Okapi brought by Capt. Boyd Alexander from the Welle River than in any other specimen seen by me. No "ossicone" or tegumentary cap has been observed in Okapi in connection with this median tumescence. Has there been one present in the ancestors of Okapi? Or does the tumescence precede the formation of a tegumentary ossicone?

Text-fig. 35.



Drawing, of the natural size, of a young foetal skull of a Giraffe, preserved in the British Museum. The foetus is at so early a stage that no trace of the future horn or ossicone is presented, and moreover the arietal bone does not form the vertex of the brain-case as in the skull drawn in text-fig. 24, p. 101. It is worthy of remark that a line drawn from the occ.-par. suture to the fronto-par. suture is in this early foetal skull almost at right angles to a line drawn from the latter to the naso-frontal suture, a condition which is even more strikingly exhibited in the adult skull of the Common Ox (*Bos*) as contrasted with that of *Ovis*, *Ovibos*, and Antilopidae. In adult Giraffe the surfaces of the frontal and parietal are more nearly parallel, and in *Okapia* quite so. It is a very curious fact that in *Bos* the whole posterior region of the brain-case formed by the parietals, which in *Okapia* stretches horizontally backwards from the fronto-parietal suture to a distance as great as that occupied by the frontal portion, is abolished! The parietals are vertical and not horizontal, and a sort of false occipital ridge is formed by the fronto-parietal suture. The very young Giraffe-foetus approaches this condition.

In answer to this question, it appears to me that the following statements are justified :—

1. Since the bony horn-core of Bovidae originates as a part of the osteogenetic tissue of the frontal bone, it cannot (according to our present knowledge) be identified without considerable qualification with the free tegumentary ossicones of Giraffidae.
2. The upgrowth (tumescence) of the frontal bone in *Okapi* and of the parietal and frontal in Giraffe, which forms the bulk of the lateral horns in those animals, is more nearly similar in nature to the bony horn-cores of Bovidae than are the ossicones of Giraffidae.
3. The frontal tumescence or upgrowth of *Okapi* cannot be considered as morphologically identical with the parietal tumescence or upgrowth of *Giraffa*.
4. The free lateral ossicone of *Giraffa* might legitimately be considered as morphologically identical with the free lateral ossicone of *Okapi*. The free tegumentary ossicone of an

ancestral form might in a series of generations shift its position from the frontal to the parietal area; and it might reasonably be admitted that the upgrowth or tumescence of the frontal ceased to develop when the parietal position was assumed by the ossicone with consequent tumescence and upgrowth of the parietal bone.

5. On the other hand, the theoretical assumption that the frontally-placed ossicone of Okapi and the parietally-placed ossicone of Giraffe are independent of one another and possibly co-exist in an ancestral form, is favoured by the fact that the Giraffe does develop a *third* well-marked ossicone in the mid-line of the frontal, and that both Okapi and Giraffe exhibit minute supernumerary growths of the kind on the cranial surface.
6. It results from these considerations that it is not possible at present to trace the lateral horns of the Okapi and the Giraffe into any close genetic relationship with those of Bovidæ—still less of Cervidæ. At the same time it is possible that the peculiar superficial element of the bony horn (the ossicone) is identical in the lateral horns of Okapi and *Giraffa*, having shifted its position backwards in the latter genus. This conclusion is not, however, by any means forced upon us since the Giraffidæ are known to have an additional ossicone—the median one; and it is therefore not without analogy that independent frontal and parietal ossicones should develop.

I am aware that it is not difficult to make assumptions by means of which a genetic relationship between the lateral horns of Giraffidæ, Bovidæ, and Cervidæ is rendered possible; but it should, I think, be clearly understood that there is at present no direct evidence to support these assumptions. It may be assumed (*a*) that a bony horn of the nature of the horn-core of the Bovidæ, or of the antler-column of Cervidæ, has in some remote ancestors of the Giraffidæ become segregated from the frontal bone of which it was a part, and acquired independent existence as a fibrous rudiment as well as independent ossification, thus establishing the independent lateral ossicone of the Giraffidæ. Or, again, it may be assumed (*b*) that in ancestors of the Bovidæ and Cervidæ, bony horns which were existing as free tegumentary products, ankylosing in mature age with subjacent cranial bones, became so ankylosed at earlier and earlier stages of development until all trace of their independent origin was lost, and they appeared to originate as growths of the frontal bone itself. The stock so endowed gave rise (it would be assumed) to Bovidæ and Cervidæ; that portion of the ancestry which retained the original method of development of free tegumentary ossicones became, on the other hand, the progenitors of the Giraffidæ.

I am not aware of any facts in the structure of living or extinct Artiodactyla which furnish an analogy for either of these processes of transformation. Nor do I think that our knowledge of the extinct forms such as *Samotherium*, *Helladotherium*, *Sivatherium*,

Bramatherium, and *Hydaspitherium*, is of a nature to assist in establishing the existence of such a remarkable transformation.

The assumption *a*—namely, that the transition was from frontal outgrowths such as Bovidae and Cervidae present, to the segregation and independence of the Giraffid ossicone—meets (it may be pointed out) with an almost insuperable obstacle in the free median frontal ossicone of the Giraffe, for which there is no forerunner in the Bovi-Cervine scheme of solid continuous outgrowths of the cranial wall. The consideration of the Lower Miocene *Protoceros* with its four pairs of horns does not help us much in this question, though its possession of a pair of parietal and of two pairs of frontal upgrowths or ‘bosses’ is significant.

*Various Positions occupied by the Paired Frontal Horns of
Cavicorn and Cervine Ruminants.*

An interesting fact in relation to the question of the identification of Giraffe’s parietal with Okapi’s frontal ossicones is that

Text-fig. 36.

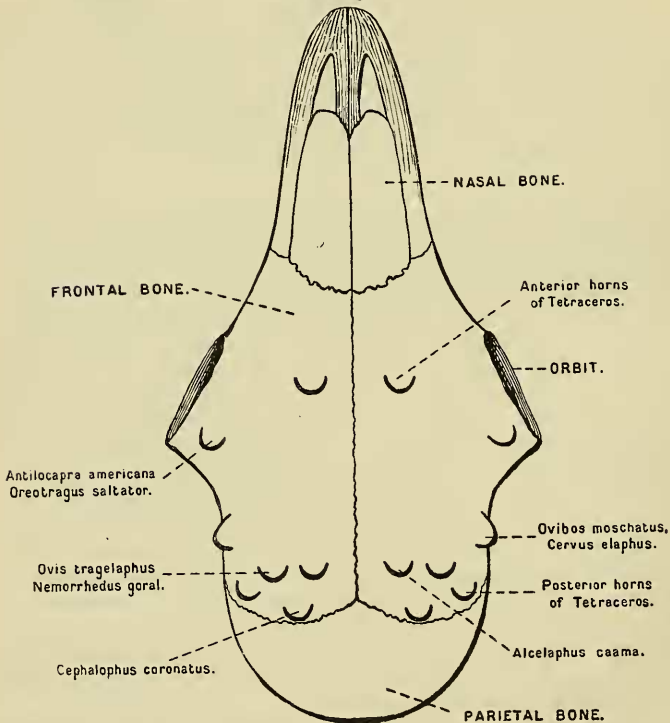


Diagram to show the various positions on the frontal bone at which the bony horn-cores of the Cavicorn and Cervine ruminants may take their growth. Though ranging widely over the frontals these upgrowths are never found as part of the parietal bones.

